SPECIES LIMITS IN THE *"SCHISTOCICHLA"* COMPLEX OF *PERCNOSTOLA* ANTBIRDS (PASSERIFORMES: THAMNOPHILIDAE)

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ABSTRACT.—The species-group in the genus *Percnostola* that is sometimes placed in the genus *"Schistocichla"* is shown to consist of seven, mostly allopatric, species. All seven are distinct morphologically; when their vocalizations were compared, 19 of 21 pairwise comparisons resulted in differences as great as or greater than those of syntopic species-pairs in this family. Differences in the two remaining comparisons were limited to two vocal characters, but one involved a pair whose ranges appear to abut without apparent physical barriers; members of the second pair were separated geographically by ~2,400 km. Insights into speciation in the complex are relevant to conservation efforts and ultimately will be related to an ongoing genetic study to suggest a phylogeny and contribute to an understanding of avian evolution in Amazonia. *Received 11 October 2005. Accepted 20 July 2006.*

The thamnophilid genus *Percnostola* is currently considered to consist of three species-groups that may not be closely related (Zimmer and Isler 2003). They include (1) a species-pair consisting of *P. rufifrons*, Black-headed Antbird, and *P. arenarum*, Allpahuayo Antbird (Isler et al. 2001); (2) a single species of uncertain affinities: *P. lophotes*, White-lined Antbird; and (3) a group of 12 taxa, sometimes placed in a distinct genus *"Schistocichla,"* that are the subject of this paper and which are referred to as the *"Schistocichla* complex."

The *Schistocichla* complex has had a confused taxonomic history since the end of the nineteenth century during which existing and newly described taxa were placed in a number of different genera and lumped or split into two or more species (sequentially: Hellmayr 1906, 1907; Cory and Hellmayr 1924; Todd 1927; Zimmer 1927; Hellmayr 1929; Zimmer 1931; Zimmer and Phelps 1946, 1947). In the process, Todd (1927) created a new genus, *Schistocichla,* for the group, but in his brief diagnosis he did not distinguish *Schistocichla* from the genus *Percnostola* to which the orig-

inal description of *leucostigma* had been assigned by von Pelzeln (1868). Finally, without explanation, Peters (1951) placed the group in the genus *Percnostola* and assigned the 12 taxa to three species: *P. schistacea* (monotypic), *P. leucostigma* (9 subspecies), and *P. caurensis* (2 subspecies). Peters (1951) decisions were followed by subsequent check-lists (Meyer de Schauensee 1966, 1970; Sibley and Monroe 1990). Ridgely and Tudor (1994) resurrected the genus *Schistocichla* for the complex, which they distinguished from other *Percnostola* species by having rounder and uncrested heads, and spots, not fringing, to their wing coverts. Although we consider it likely that *Schistocichla* ultimately will be restored for the group, we consider this diagnosis inadequate for reasons provided in Braun et al. (2005). We maintain the complex in *Percnostola* pending completion of genetic analysis of species in *Percnostola* and related genera, after which the morphological, vocal, and genetic analyses will be integrated to suggest a phylogeny and an appropriate generic name.

Generic placement of the *Schistocichla* complex is not essential to the present analysis of species limits. The careful definition of species is of vital concern, however, for conservation efforts and is essential for phylogenetic study and reconstruction of the historical processes leading to the distribution of biota in Amazonia. Previously, species and subspecies in the group were defined by the sympatry of

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P. schistacea and *P. leucostigma*, and by morphological characters. To these considerations, this paper adds vocal characters and newly obtained biogeographic knowledge. Vocalizations are valuable indirect measures of gene flow and species limits (Johnson et al. 1999, Helbig et al. 2002, Remsen 2005) for antbirds and other suboscine passerines in which vocalizations are thought not to be learned (Isler et al. 1998, Baptista and Kroodsma 2001). The objective of this paper is to use vocal characters to improve understanding and recognition of species limits in the *Schistocichla* complex.

METHODS

The *Schistocichla* complex of *Percnostola* antbirds (Zimmer and Isler 2003) consists of: *P. leucostigma*, Spot-winged Antbird, which includes nine subspecies (*P. l. subplumbea, P. l. obscura, P. l. saturata, P. l. leucostigma, P. l. intensa, P. l. brunneiceps, P. l. infuscata, P. l. humaythae,* and *P. l. rufifacies*); *P. schistacea*, Slate-colored Antbird, considered monotypic; and *P. caurensis*, Caura Antbird, with two subspecies (*P. c. caurensis* and *P. c. australis*). Vocal recordings of *P. l. intensa* and *P. c. caurensis* were unavailable for this study. The remaining 10 taxa are maintained as units of analysis, and we use "*schistacea*," "*caurensis*" and subspecies names of *P. leucostigma* (without initials of genus or species) to reference populations.

The definition of geographic units for the analysis began with published distributional boundaries (Fig. 1A, B). However, because of the possibility that plumage-based subspecies distributions may not fully express the existence of independently evolving populations as may be reflected in their vocalizations, ranges of *P. leucostigma* subspecies were divided further into 30 geographic clusters (Fig. 1C) based on knowledge of the biogeography of other thamnophilid antbirds. For example, if a river was known to define ranges of other closely related pairs of thamnophilid taxa, recordings obtained on opposite sides of that river were separated into clusters. Geographic clustering of *humaythae* recordings also took into consideration that *P. leucostigma* "*major*" Todd (1927) had been described from the region immediately south of the Amazon but synonymized with *humaythae* by Hellmayr

(1929). We compared vocal data for adjacent geographic clusters and aggregated clusters in which vocalizations did not differ diagnosably. Thus, *P. leucostigma* clusters were gradually consolidated until the aggregated populations evidenced diagnostic vocal differences. Similarly, the smaller geographic range of *P. schistacea* was divided initially into three clusters to test for geographic variation. Recordings of *P. caurensis* were available from only one location (Zimmer 1999).

Vocal characters used to examine species limits were: (1) number of notes, (2) duration, (3) pace, (4) change of pace, (5) note shape, (6) change in note shape, (7) note length, (8) change in note length, (9) interval length, (10) change in interval length, (11) peak frequency, and (12) change in peak frequency (Appendix 1). Conceptually, these characters were considered independent from one another; variation in one character could occur without resulting in a different outcome for another character. We also recognized the possibility, however, that some characters might be linked, given their likely common ancestry. Consequently, we culled pairs of character measurements that had correlation coefficients ≥0.80.

Tape recordings (391 recordings from 265 localities) were compiled from natural sound archives, from our personal inventories, and from unarchived contributions from other individuals (Appendix 2). We reviewed every recording to identify the number and gender of individuals vocalizing and to label every vocalization as to type. Loudsongs (following Willis 1967) refer to the ringing series of notes delivered in a consistent pattern that is often described simply as song. Canary 1.2 and Raven 1.2 (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Ithaca, New York, USA) were used to make a spectrogram of every vocalization type delivered by each individual of either gender on every recording. Qualitative characters were obtained by examining printed copies of all clearly delineated spectrograms (i.e., sampling was not used). We considered a qualitative character to be diagnostic when visual examination completely distinguished every spectrogram of one population from another. If there was any uncertainty, we conducted "blind tests." Spectrograms were stripped of
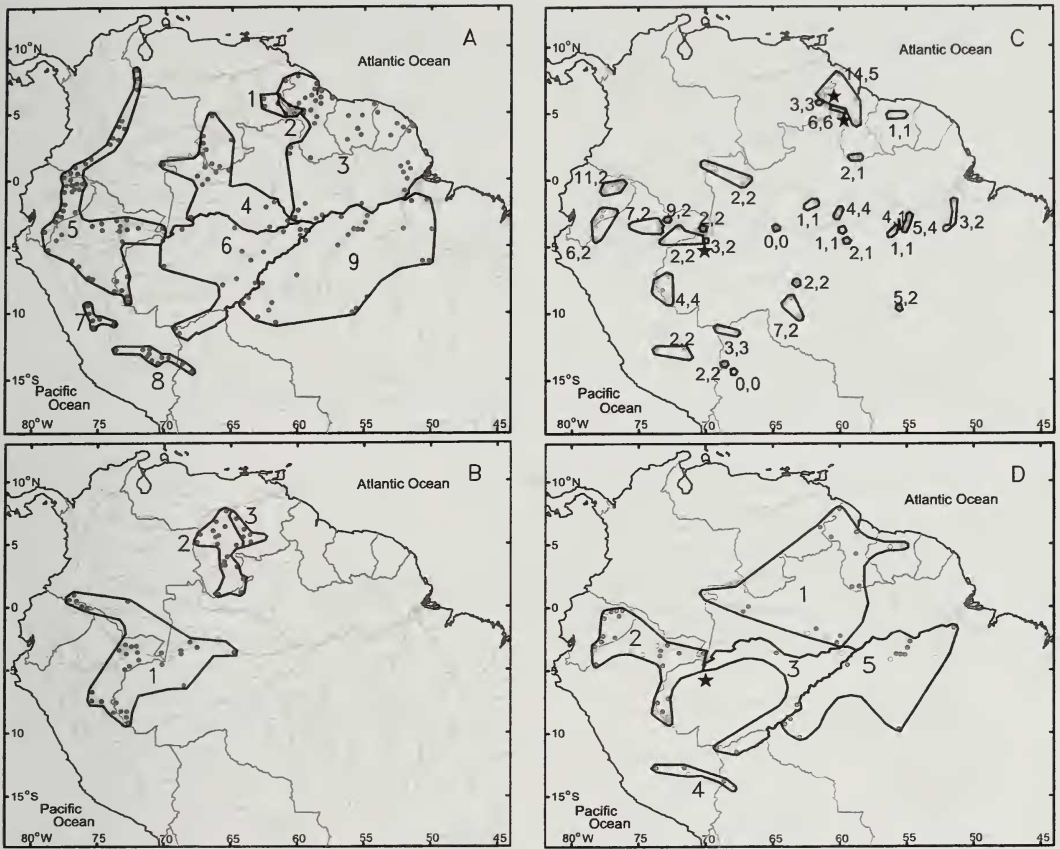
FIG. 1. Geographic ranges and recording locations. Locations are assigned to geographic sectors (Isler 1997). (A) Known geographic ranges of nine taxa considered by Peters (1951) to be subspecies of *Percnostola leucostigma*. 1 = *P. l. obscura*; 2 = *P. l. saturata*. 3 = *P. l. leucostigma*; 4 = *P. l. infuscata*; 5 = *P. l. subplumbea*; 6 = *P. l. humaythae*; 7 = *P. l. intensa*; 8 = *P. l. brunneiceps*; 9 = *P. l. rufifacies*. Solid circles = locations documented by specimens, recordings, photographs, or records by experienced observers. (B) Known geographic ranges of the three remaining taxa in the *Schistocichla* complex. 1 = *Percnostola schistacea*; 2 = *P. caurensis australis*; 3 = *P. c. caurensis*. Symbols as in Fig. 1A. (C) Initial stage locations, number of recordings, and sample sizes of male loudsongs in *P. leucostigma* populations (including *saturata* and *obscura*) analyzed as populations. Solid circles = recording locations of male loudsongs. Open circles = recording locations of other vocal types. Stars = locations where vocally distinct populations were found to be parapatric. Numbers = total number of male loudsong recordings followed by sample size. (D) Final stage locations of recordings of five taxa currently considered subspecies of *P. leucostigma*. Symbols as in (C). Lines encircle recordings ascribed to taxa: 1 = *leucostigma*; 2 = *subplumbea*; 3 = *humaythae*; 4 = *brunneiceps*; 5 = *rufifacies*.

any identification except a randomly selected code number, sorted visually according to perceived differences, and considered to differ diagnosably only if the resultant groups distinguished populations unequivocally.

Calls were used solely as discreet characters (presence/absence in population repertoires and qualitative differences in note shape). Quantitative characters were restricted to a sample of loudsong recordings. Sample sizes reflect number of individuals, not number of vocalizations measured. We measured three vocalizations of each vocalization type for at least six individuals of every population, although it was not possible to achieve this goal because of recording inadequacies. If more than six suitable recordings were available, we sought to distribute the sample throughout the region defined for the population. Quantitative measures were obtained from spectrograms projected on a 43-cm screen from a Macintosh G4 computer using default settings of Canary

1.2 (Charif et al. 1995), except the display was set to smooth, overlap was adjusted from 50 to 93.7% depending on recording quality, and contrast was adjusted according to recording intensity with care taken to retain all elements of the vocalization. These were supplemented by recordings projected on a 43-cm screen by a Dell 8300 computer using parallel settings of Raven 1.2 (Charif et al. 2004). Cursor measurements were typically at scales of 0.12 sec/cm and 1.5 kHz/cm.

Diagnostic differences must be discrete, non-overlapping character states that have the potential for unambiguous signal recognition (Isler et al. 1998, 1999). Ranges of samples of continuous variables could not overlap, and the likelihood that ranges would not overlap with larger sample sizes was estimated by requiring the means ($\bar{x}$) and standard deviations (SD) of the population with the smaller set of measurements (a) and the population with the larger set of measurements (b) to meet the test:

$$\bar{x}_a + t_a SD_a \leq \bar{x}_b - t_b SD_b$$

where t_i = the t-score at the 97.5 percentile of the t distribution for $n - 1$ degrees of freedom. A similar test could not be used for ratios, which are not distributed normally, and a non-parametric bootstrap simulation was used to examine statistical significance. We compared the difference between the means (DBM) for the two taxa being analyzed and the two groups of generated data of the same sample sizes. The method generated 10,000 sample population pairs, with replacement, and compared the DBM between the two compared species to the distribution of DBMs of the simulated populations. The result was distributed normally, and significance assigned according to the rules of this distribution.

We assessed taxonomic status based on vocal distinctions, accepting current subspecies definitions as reflecting diagnostic morphological differences. We recommended species status for populations that differed diagnostically in both vocalizations and morphology. Vocal differences were considered diagnostic at the species level if the analysis revealed three or more diagnostic vocal characters (Isler et al. 1998). This guideline has been recognized as a relevant "yardstick" in considering species status for allopatric thamnophilid populations (Johnson et al. 1999, Helbig et al. 2002, Remsen 2005). Fewer vocal characters were considered acceptable when populations were parapatric without obvious geographic barriers or highly differentiated morphologically. Existing taxa that did not meet vocal requirements for recommendations as distinct species were maintained as subspecies pending results of an ongoing molecular study.

RESULTS

Loudsongs.—Most vocal differences among taxa occurred in their loudsongs (Fig. 2). Males and females gave similarly structured loudsongs, although female loudsongs tended to have fewer notes and to be slower paced. Only loudsongs that could be attributed to males were used in the analysis because too few recordings of loudsongs were clearly identified as being delivered by females.

No vocal differences were found between *obscura* and *saturata* of the Gran Sabana region of southeastern Venezuela and adjacent Guyana (Fig. 1A). Their vocal data were aggregated in this study under the name of *saturata* which has priority. When loudsongs of *saturata* were compared to the remaining taxa in the "*Schistocichla*" complex (Table 1, Appendix 1), they differed diagnostically in at least five vocal characters in each pair-wise comparison with one exception, the *saturata-brunneiceps* comparison. Only two vocal characters, visual differences in "long calls" and patterns of peak frequencies of loudsongs, differed diagnosably between *saturata* and *brunneiceps*. Measurements of three additional loudsong characters (pace, note length, and peak frequency) did not overlap, but our statistical test suggested that overlap was possible with larger samples.

Nominate *leucostigma*, *infuscata*, *subplumbea*, and *humaythae* are distributed around northern and western Amazonia (Fig. 1A). Recordings of *infuscata* were merged into *leucostigma* in the final analysis because we found no diagnostic differences between them. No vocal differences were identified within the range of *humaythae* after dividing recordings north and south of seven degrees South latitude (samples from the south, $n = 7$, included two recordings from the type locality of *humaythae*; samples from the north,
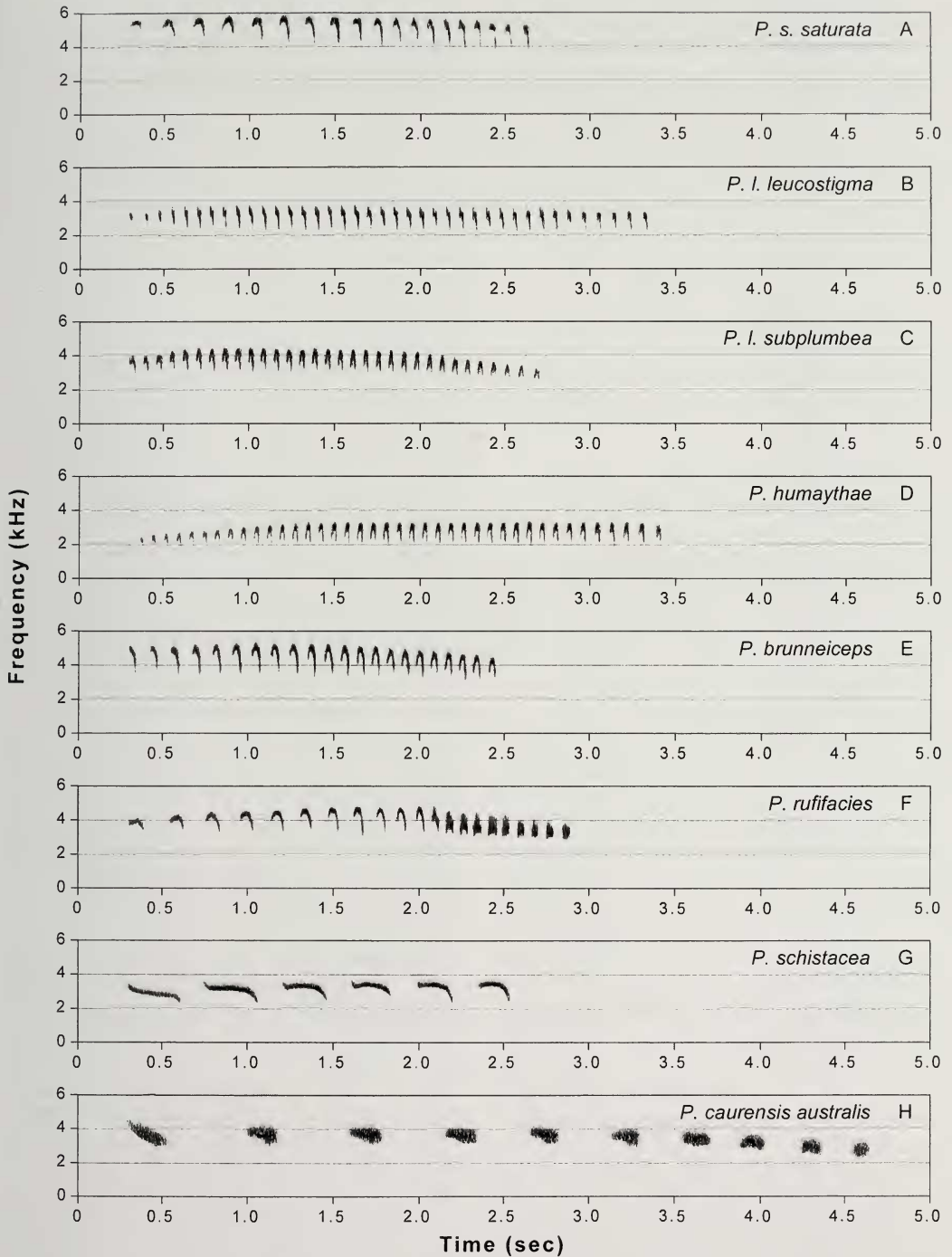
FIG. 2. Loudsongs of taxa in the "*Schistocichla*" complex. Nomenclature follows recommendations of this paper. (A) *P. s. saturata*, Kaieteur Fall, Guyana (ISL-MJB.001:40). (B) *P. l. leucostigma*, Manaus region, Amazonas, Brazil (ML 74353). (C) *P. l. subplumbea*, La Selva Lodge, Napo, Ecuador (ISL-RAB.001:11). (D) *P. humaythae*, Camino Mucden, Pando, Bolivia (ML 38882). (E) *P. brunneiceps*, Amazonia Lodge, Madre de Dios, Peru (ISL-JCA.008.01). (F) *P. rufifacies*, Itapoama, Pará, Brazil (ISL-BMW.101:34). (G) *P. schistacea*, Igarapé Ouro Preto, Acre, Brazil (ISL-BMW.138:18). (H) *P. caurensis australis*, Serranía de Cerbatana, Bolívar, Venezuela (ISL-KJZ.064:12). (Archive acronyms in Appendix 2.)

TABLE 1. Diagnostic vocal characters distinguishing male loudsongs and calls of *Percnostola* taxa for which diagnosable differences were found. Nomenclature follows recommendations of this paper. Recordings were unavailable for *P. l. intensa* and for the nominate form of *P. caurensis*, vocalizations of *P. s. saturata* and *P. s. obscura* were indistinguishable, and vocalizations of *P. l. leucostigma* and *P. l. infuscata* were indistinguishable. Sample sizes reflect number of individuals.

Taxa	n	P. l. leucostigma	P. l. subplumbea	P. humaythae	P. brunneiceps	P. rufifacies	P. schistacea	P. caurensis australis
P. saturata	16	6	6	6	2	5	9	7
P. l. leucostigma	5		1	1	4	7	7	8
P. l. subplumbea	8			2	4	7	7	7
P. humaythae	16				4	8	8	9
P. brunneiceps	18					4	9	6
P. rufifacies	12						8	6
P. schistacea	6							8
P. caurensis australis	13							

$n = 5$, included three recordings from the south bank of the Amazon near the type locality of "*major*"). Vocal distinctions among *leucostigma* (including *infuscata*), *subplumbea*, and *humaythae* loudsongs (sample distributions Fig. 1D) were found in peak frequency and the pattern of peak frequency change. Peak frequency levels of *humaythae* loudsongs were lower throughout the first half of the loudsong, as exemplified by the second note (Fig. 3A), diagnostically when compared to *subplumbea*, but not to *leucostigma*. Differing patterns of peak frequency change were apparent visually (Fig. 2). Peak frequencies of *leucostigma* notes were nearly constant (although often rising slightly at the beginning and dropping slightly at the end); those of *subplumbea* increased and decreased in frequency; whereas those of *humaythae* increased initially and then flattened out (although sometimes dropping slightly in the final few notes). These differences were expressed quantitatively (Fig. 3B); the ratio of the peak frequency of the second note divided by that of the penultimate note differed diagnostically between *leucostigma* and *subplumbea* and between *subplumbea* and *humaythae*.

The remaining three subspecies of *P. leucostigma* (*intensa, brunneiceps,* and *rufifacies*) are distributed along the base of the Andes in Peru and Bolivia and east of the Rio Madeira in Brazil (Fig. 1A; sample distributions Fig. 1D). Of these, vocalizations of *rufifacies* were most distinct, and a shift in note shape near the midway point of its loudsong was unique (Fig. 2). A mean difference of 6.0 vocal characters distinguished *rufifacies* from other taxa currently considered subspecies of *P. leucostigma* (Table 1). Four vocal characters distinguished loudsongs of *brunneiceps* from all other *leucostigma* subspecies except *saturata* (Table 1); both *brunneiceps* and *saturata* had loudsongs that initially were slowly paced and then accelerated (Fig. 2). Vocal recordings of *intensa* were unavailable.

The final three taxa in the assemblage have been placed in two species, the monotypic *schistacea* and *caurensis* including the subspecies *australis* (Fig. 1B). Loudsongs of *schistacea* were disaggregated into three geographic clusters to investigate the possibility that it was a polytypic species. Loudsongs recorded north of the Amazon tended to be
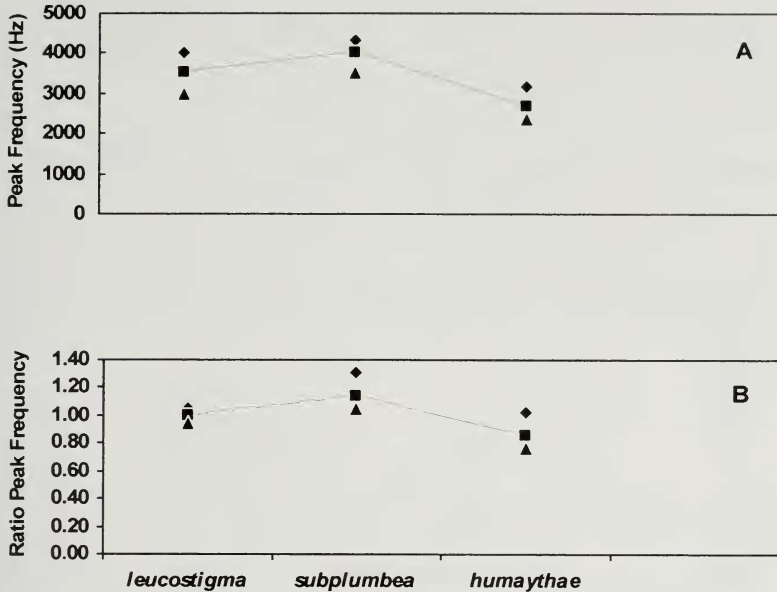
FIG. 3. Selected frequency characteristics of loudsongs of *leucostigma, subplumbea*, and *humaythae* arranged geographically from northeast to northwest to southwest (Fig. 1A). Lines connect means. Symbols above and below line reflect maximum (diamond) and minimum (triangle) values. (A) Frequency level as reflected in the peak frequency of the second note in the loudsong. (B) Pattern of frequency change as measured by the ratio of the peak frequency of the second note divided by that of the penultimate note.

slower paced with corresponding longer terminal notes than those recorded immediately south of the river. These differences did not meet our statistical test, and loudsongs from the extreme southern portion of its range (Acre, Brazil) were intermediate. Vocalizations of *schistacea* were aggregated for the final analysis. Vocal data were available for *caurensis* from only one location. Numerous diagnostic differences in loudsong structure between *schistacea* and *caurensis*, and between each and the remaining taxa were apparent in visual examinations (Fig. 2) and quantitative vocal characters (Table 1).

Calls.—Vocal repertoires of all taxa included a "long call," a descending whistle sounding like *teeeeur* (Fig. 4A–C). The figure illustrates the variety of forms of this call, and we identified no diagnostic differences among taxa with two exceptions. The long call of *saturata* ($n = 9$) was preceded by an abrupt note at a higher pitch (Fig. 4D), and that of *caurensis* ($n = 10$) was strongly frequency modulated and consistently included an overtone (Fig. 4E). A second principle type was a "short call" consisting of multiple, closely

spaced vertical elements and imparting a vibrating quality, sounding like *tchick* (Fig. 4F). It was given by all taxa. The single recording of the short call of *caurensis* appeared to be simpler structurally, but the difference was not considered diagnostic pending acquisition of additional recordings. The third principle type of call consisted of a narrow vertical note repeated in short series of 3–14 notes having the quality of a "rattle" (Fig. 4H). No differences in the rattle were diagnosed among taxa. The long call, short call, and rattle were frequently intermixed and delivered in rapid succession by birds of both gender.

Beyond the three principal types of calls, a "multi-note series" was recorded for some taxa. In *rufifacies*, this was a repetition of the long call (Fig. 4J). In *leucostigma* and *subplumbea*, however, a short series was recorded in which the initial part of the note rises, forming an inverted "U" (Fig. 4K), and a similar call was recorded for *schistacea* (Fig. 4L). A larger sample of recordings may reveal diagnostic differences among taxa in the multi-note series. Finally, *schistacea* was found to have a fifth type in its repertoire, a "chevron
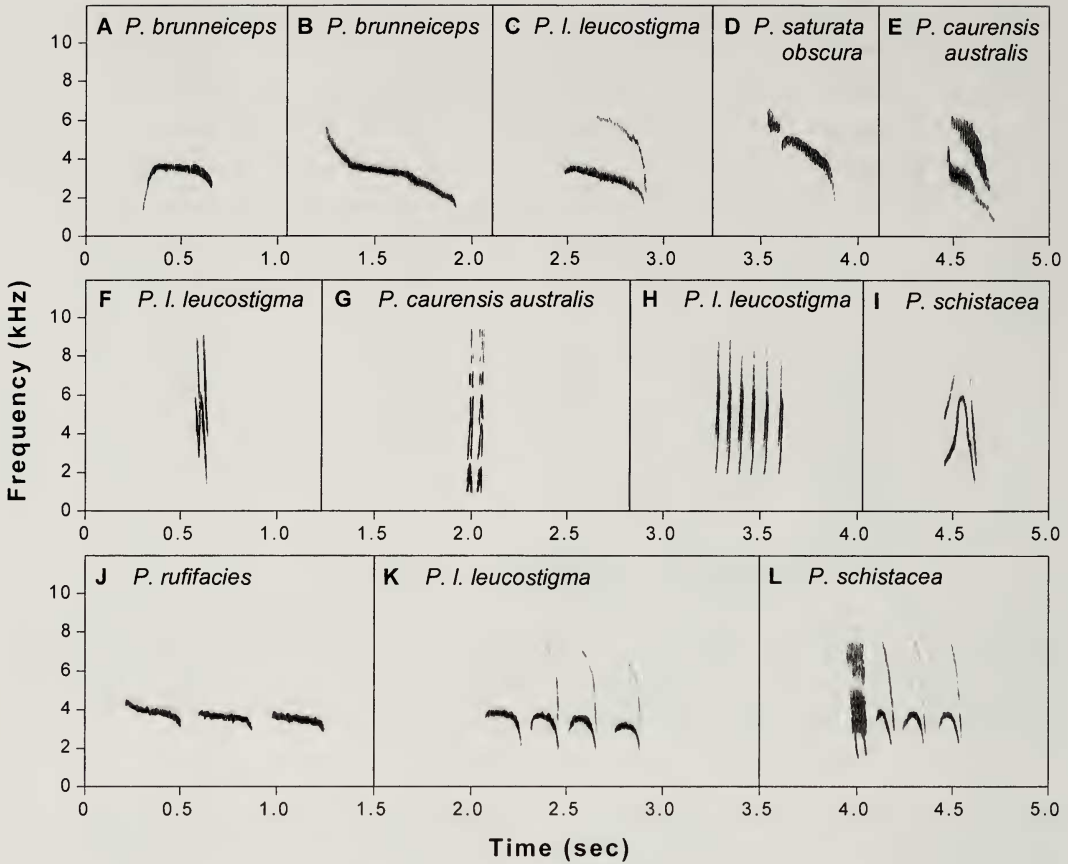
FIG. 4. Calls of taxa in the "*Schistocichla*" complex. Nomenclature follows recommendations of this paper. (A) Long call *P. brunneiceps*, Amazonia Lodge, Madre de Dios, Peru (ISL-BMW.031:13). (B) Long call *P. brunneiceps*, Río Tuichi, La Paz, Bolivia (ISL-BMW.117:31). (C) Long call *P. l leucostigma*, La Escalera, lower elevations, Bolívar, Venezuela (NSA 26680). (D) Long call *P. saturata obscura*, La Escalera, upper elevations, Bolívar, Venezuela (NSA 68312). (E) Long call *P. caurensis australis*, Serranía de Cerbatana, Bolívar, Venezuela (ISL-KJZ.063:27). (F) Short call *P. l. leucostigma*, Manaus region, Amazonas, Brazil (ML 74353). (G) Short call *P. caurensis australis*, Serranía de Cerbatana, Bolívar, Venezuela (ISL-KJZ.063:22). (H) Rattle *P. l. leucostigma*, La Escalera, lower elevations, Bolívar, Venezuela (NSA 26680). (I) Chevron-shaped call *P. schistacea*, Quebrada Sucusari, Loreto, Peru (ML 47797). (J) Multi-note call *P. rufifacies*, Itapoama, Pará, Brazil (ISL-BMW.101:34). (K) Multi-note call *P. l. leucostigma*, Dubulay Ranch, Guyana (ISL-MBR.002.01). (L) Multi-note call *P. schistacea*, P. N. Serra do Divisor, Acre, Brazil (ISL-BMW.128:20).

shaped call," (Fig. 4I) that was unique in the complex.

New Geographic Information.—Recent field studies have documented two cases of apparent parapatry of taxa in the "*Schisto-cichla*" complex. First, *saturata* and *leucos-tigma* have been found to be parapatric in Guyana and eastern Venezuela. Second, we tape-recorded two taxa along the right bank of the lower Rio Javari, Amazonas, Brazil. At the Reserva Natural Palmarí (04° 17′ S, 70° 18′ W), loudsongs were typical of *subplumbea*, whereas near the mouth of the Rio Javari in the vicinity of Benjamin Constant (04° 22′ S, 70° 02′ W), loudsongs matched those of *hu-maythae*. The distance between the two sites is approximately 60 km with no obvious to-pographic barrier between them, suggesting parapatry or the possibility of sympatry.

DISCUSSION

We propose the following taxonomic posi-tions and English names for members of the

complex. The sequence of species is tentative, awaiting genetic analysis.

Percnostola saturata (Salvin)—Roraiman Antbird
    P. s. saturata (Salvin)
    P. s. obscura (Zimmer and Phelps)
Percnostola leucostigma von Pelzeln—Spot-winged Antbird
    P. l. leucostigma von Pelzeln
    P. l. infuscata (Todd)
    P. l. subplumbea (Sclater and Salvin)
    P. l. intensa (Zimmer)
Percnostola humaythae (Hellmayr)—Humaita Antbird
Percnostola brunneiceps (Zimmer)—Brownish-headed Antbird
Percnostola rufifacies (Hellmayr)—Rufous-faced Antbird
Percnostola schistacea (Sclater)—Slate-colored Antbird.
Percnostola caurensis (Hellmayr)—Caura Antbird
    P. c. caurensis (Hellmayr)
    P. c. australis (Zimmer and Phelps)

Our results for *saturata* were consistent with those of Braun et al. (2005) who recommended species status based on morphological and genetic differences as well as a smaller sample of vocalizations than was used in this study. A large number of vocal characters distinguished *saturata* from all taxa except *brunneiceps* (Table 1). Vocal differences between *saturata* and *brunneiceps* came close to meeting our guideline, however. The wide geographic disjunction of their ranges (~2,400 km) suggests that *saturata* and *brunneiceps* have evolved independently and that loudsong similarities are homoplasious. Species status for *brunneiceps* was supported by the finding that it differed from the remaining taxa by an average of five and a minimum of four vocal characters.

The fewest vocal differences were found among *leucostigma*, *subplumbea*, and *humaythae* (Table 1). However, assessment of taxonomic status must also consider geographic relationships. The geographic pattern of values of vocal characters (Fig. 3) is inconsistent with a cline, with values rising between *leucostigma* and *subplumbea* and decreasing sharply between *subplumbea* and *humaythae*. Clinal variation in a vocal character of another

thamnophilid antbird was documented to correspond with genetic intergradation (Isler et al. 2005), and the lack of clinality indicated an absence of intergradation. The conclusion that *subplumbea* and *humaythae* were specifically distinct was buttressed by apparent parapatry along the Rio Javari. Vocal differences between *subplumbea* and nominate *leucostigma* were insufficient, however, to raise *subplumbea* to the species level. Also best maintained as subspecies of *leucostigma* are *infuscata*, for which no diagnostic vocal differences with *leucostigma* were identified, and *intensa*, for which no vocal recordings were available. The latter is based on plumage similarities, although future vocal and genetic analyses may reveal that *intensa* is related to *brunneiceps* as both taxa occur in Andean foothills. Our results supported Hellmayr's (1929) conclusion that "*major*" (Todd 1927) is a synonym of *humaythae*.

Large numbers of vocal characters distinguished *rufifacies*, *schistacea*, and *caurensis* which are considered specifically distinct. Of the taxa currently considered subspecies of *P. leucostigma*, *rufifacies* was most dissimilar vocally and differed from the other taxa by an average of 7.9 and a minimum of five vocal characters (Table 1). The two taxa, *schistacea* and *caurensis*, currently accepted as distinct species (Peters 1951, Sibley and Monroe 1990), differed by a minimum of five vocal characters and averages of 10.0 and 9.0, respectively. Analysis of vocal variation within the range of *schistacea* indicated that it was best maintained as a monotypic species.

Two currently named subspecies are dubiously distinct but are maintained pending acquisition of vocal and/or genetic materials. Hilty (2003 and pers. comm.) examined a large series of specimens at the Museo de Phelps and concluded that *P. c. australis* did not differ appreciably from the nominate form and was not worthy of recognition. We also follow Braun et al. (2005) in maintaining *obscura* as a subspecies of *P. saturata* pending genetic analysis.

Future Work.—Further recommendations regarding taxonomic status and estimation of the phylogeny of the *Schistocichla* complex await completion of the genetic study now underway. Vocal analysis of additional recordings would be valuable, especially recordings

that permit *P. l. intensa* to be included in the analysis. Comparison of the behavioral context and evolution of vocalizations with those of other thamnophilid groups should be rewarding. For example, the similarity of calls among different populations and species in the *Schistocichla* complex was in stark contrast to the distinctive qualities of calls in the *Hypocnemis cantator* complex, another widespread Amazonian group of antbirds (Isler et al. 2007). A thorough understanding of geographic variation in the *Schistocichla* complex offers a potentially valuable window on avian evolution in the Neotropics but requires additional field work, including the collection of specimens, tissue, behavioral information, and vocal recordings from regions in which these are currently unknown.

ACKNOWLEDGMENTS

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APPENDIX 1

Pairwise comparisons of vocal characters diagnosing male loudsongs and calls of populations in the "*Schistocichla*" complex. Sequence follows Table 1 from left to right and top to bottom. All measured characters refer to loudsongs; differences among calls were diagnosed solely by presence/absence of a type of call and by note shape.

Vocal characters were defined as follows:

(1) Number of notes: inclusive of all notes. (2) Duration: time (sec) from beginning of first note to end of ultimate note. (3) Pace: notes/sec, measured from beginning of first note to end of ultimate interval. (4) Change of pace: notes and following intervals were separated into three sections most equivalent in time, pace was computed for each section, and ratios were used to compare sections. Sections are labeled 1, 2, and 3, consecutively, and 1/3, for example, indicates section 1 divided by section 3. (5) Note shape: qualitative, defined in the following paragraph. (6) Change in note shape: qualitative. (7) Note length: lengths in millisec of first, second, middle, penultimate, and ultimate notes, labeled 1 through 5 consecutively. (8) Change in note length: comparisons of note lengths expressed in ratios; 1/5, for example, indicates note 1 divided by note 5. (9) Interval length: lengths in millisec of intervals following first, second, middle, and penultimate notes, labeled 1 through 4 consecutively. (10) Change in interval length: comparisons of interval lengths expressed in ratios; 1/4, for example, indicates interval 1 divided by interval 4. (11) Peak frequency: the highest frequencies attained by first, second, middle, penultimate, and ultimate notes. Numerical labels same as for notes. (12) Change in peak frequency: comparisons of peak frequencies expressed in ratios; numerical labels same as for change in note length.

We used the following terms in describing note shape. "Downslurred" indicates a decrease in note frequency (i.e., the spectrogram trace goes from a higher to a lower frequency). An "upslurred" note goes in the opposite direction. A "flat" note shows little or no change in frequency (a horizontal line on the spectrogram). Frequency gradually increases and decreases in a "rounded" note. A "chevron" resembles an inverted V with a sharp point at the highest frequency. "Frequency-modulated" notes produce a spectrogram trace similar to a "zig-zag" sewing machine stitch within the confines of the general shape of the note. "Clear" notes are represented on a spectrogram by tracings with distinct edges, whereas a note lacking a clear shape is "poorly defined". "Note shape pattern" describes how the shapes of notes change throughout a multi-note vocalization.

Visual identifications of frequency pattern were in reference to a horizontal line drawn through the frequencies of the vocalization. "Peak frequency" refers to the highest frequency attained by the main body of an individual note. "Peak frequency pattern" describes how the highest frequencies of notes change through the course of a multi-note vocalization. "Increase," "flat," and "decrease" refer to changes of peak frequencies among the notes in a series.

saturata versus *leucostigma*.—(1) Change of pace: *leucostigma* accelerates at beginning and decelerates at end; *saturata* accelerates throughout and at a faster rate at beginning as measured in pace ratio of sections 1/2, 1/3, 2/3. (2) Note duration: *leucostigma* notes are shorter initially as measured in length of note 2. (3) Interval duration: *leucostigma* intervals are shorter throughout most of loudsong as measured in length of interval 2. (4) Peak frequency: *leucostigma* lower throughout loudsong as measured in peak frequency of notes 1, 2, 3, 4, 5. (5) Change in peak frequency: *leucostigma* increases and decreases gradually; *saturata* first half is flat or increases gradually and then decreases sharply as measured in ratio of peak frequencies 2/5. (6) Long Call: note shape differs.

saturata versus *subplumbea*.—(1) Pace: *saturata* is slower as measured in pace sections 1, 2. (2) Change of pace: *saturata* accelerates throughout and at a faster rate at beginning; *subplumbea* accelerates at beginning and decelerates at end as measured in pace ratio of sections 1/2, 1/3, 2/3. (3) Change in note length. *saturata* notes shorten; *subplumbea* lengthen or are nearer to even as measured in ratio of notes 1/4, 1/5. (4) Peak frequency: *saturata* higher throughout loudsong as measured in peak frequency of notes 1, 2, 3, 4, 5. (5) Change in peak frequency: *saturata* first half is flat or increases slightly; *subplumbea* first half increases more obviously as measured in ratio of peak frequencies 2/3. (6) Long Call: note shape differs.

saturata versus *humaythae*.—(1) Pace: *saturata* is slower as measured in pace sections 1, 2, 3. (2) Change of pace: *saturata* accelerates throughout and at a faster rate at beginning; *humaythae* accelerates at beginning and decelerates at end as measured in pace ratio of sections 1/2, 1/3, 2/3. (3) Change in note

duration: *saturata* notes shorten or are close to even; *humaythae* notes lengthen in first half of loudsong as measured in ratio of notes 2/3, 2/4. (4) Peak frequency: *saturata* higher throughout loudsong as measured in peak frequency of notes 1, 2, 3, 4, 5. (5) Change in peak frequency: *saturata* initially flat or increases slightly, then decreases sharply; *humaythae* increases sharply in first quarter of song, then is flat although terminal notes decrease as measured in ratio of peak frequencies 1/3, 1/4, 1/5, 2/3, 2/4, 2/5. (6) Long Call: note shape differs.

saturata versus *brunneiceps*.—(1) Change in peak frequency: distinguished by the slower pace of *saturata* (no overlap with *brunneiceps* but statistically not significant given current samples) combined with the steeper decrease in frequency in the final third. (2) Long Call: note shape differs.

saturata versus *rufifacies*.—(1) Note shape: although notes of both are more or less chevron-shaped, notes of *rufifacies* are clearly downslurred throughout first half of songs whereas those of *saturata* only occasionally lack upslur in first few notes. (2) Change in note shape: *saturata* notes maintain clear shape; *rufifacies* become frequency modulated. (3) Peak frequency: *saturata* higher throughout loudsong as measured in peak frequency of notes 1, 2, 3, 4, 5. (4) Change in peak frequency: *saturata* final notes decrease gradually although somewhat sharply; *rufifacies* final notes decrease abruptly and sharply. (5) Long Call: note shape differs.

saturata versus *schistacea*.—(1) Number of notes: fewer notes in *schistacea* loudsong. (2) Note shape: *schistacea* notes are flat or slightly rounded; *saturata* notes are chevron shaped. (3) Change in note shape: *schistacea* notes become more rounded and downslurred; *saturata* notes maintain shape although initial notes sometimes lack upslur side of chevron. (4) Interval duration: *schistacea* interval 4 longer. (5) Change in interval duration: *schistacea* intervals near even in length; *saturata* intervals shorten more as measured by ratios of intervals 1/3, 1/4, 2/4. (6) Peak frequency: *schistacea* notes 1, 2, 3, and 4 lower. (7) Change in peak frequency: in second half of loudsong *schistacea* notes increase gradually or are flat; second half notes of *saturata* notes decrease to a level lower than initial notes as

measured by ratios of peak frequencies 1/4, 1/5, 2/4, 2/5, 3/4, 3/5. (8) Long call: Note shape differs. (9) Chevron-shaped call: found only in *schistacea*.

saturata versus *caurensis*.—(1) Note shape: *caurensis* notes are heavily frequency modulated and poorly defined; *saturata* notes are chevron shaped. (2) Change in note shape: *caurensis* notes are slightly downslurred initially, but then slightly rounded or shapeless; *saturata* notes maintain shape although initial notes sometimes lack upslur side of chevron. (3) Note duration: *caurensis* notes are longer throughout as measured in length of notes 1, 2, 3, 4, 5. (4) Interval duration: *caurensis* intervals are longer throughout most of loudsong as measured in length of intervals 1, 2. (5) Peak frequency: *caurensis* lower throughout loudsong as measured in peak frequency of notes 1, 2, 3, 4, 5. (6) Change in peak frequency: *caurensis* first half is flat or decreases gradually and then decreases sharply; *saturata* initially flat or increases slightly, then decreases sharply as measured in ratio of peak frequencies 1/4, 1/5, 2/4, 2/5, 3/4, 3/5. (7) Long Call: note shape differs.

leucostigma versus *subplumbea*.—(1) Change in peak frequency: *leucostigma* loudsongs are mostly flat, increasing and decreasing slightly; *subplumbea* loudsongs decrease sharply in the final quarter as measured in ratio of peak frequencies 2/4, 3/4.

leucostigma versus *humaythae*.—(1) Change in peak frequency: *leucostigma* increases and decreases gradually; *humaythae* increases sharply in first quarter of song, then is flat although terminal few notes may decrease slightly as measured in ratio of peak frequencies 1/3, 2/3.

leucostigma versus *brunneiceps*.—(1) Change of pace: *leucostigma* accelerates at beginning and decelerates at end; *brunneiceps* accelerates throughout as measured in pace ratio sections 1/3, 2/3. (2) Change in interval duration: *leucostigma* near even spacing; *brunneiceps* shortens as measured in ratio of intervals 1/4. (3) Peak frequency: *leucostigma* lower throughout much of loudsong as measured in peak frequency of notes 1, 2, 3. (4) Change in peak frequency: *leucostigma* increases and decreases gradually; *brunneiceps* first half to two-thirds flat or nearly so, remaining notes

decrease sharply as measured in ratio of peak frequencies 1/4, 1/5, 2/4, 2/5, 3/5.

leucostigma versus *rufifacies*.—(1) Change of pace: *leucostigma* accelerates at beginning and decelerates at end; *rufifacies* accelerates throughout and at a faster rate at beginning as measured in pace ratio of sections 1/2, 1/3, 2/3. (2) Note shape: although notes of both are more or less chevron-shaped, notes of *rufifacies* are more strongly downslurred throughout first half of the vocalization. (3) Change in note shape: *leucostigma* notes maintain clear shape; *rufifacies* become frequency modulated. (4) Note duration: *leucostigma* notes are shorter initially as measured in length of note 2. (5) Change in note duration: *leucostigma* notes lengthen or are close to even; *rufifacies* notes shorten as measured in ratio of notes 2/3. (6) Interval duration: *leucostigma* intervals are shorter throughout most of loudsong as measured in length of intervals 1, 2, 3. (7) Change in peak frequency: *leucostigma* increases and decreases gradually; *rufifacies* increases gradually in first half to two-thirds, remaining notes decrease abruptly and sharply.

leucostigma versus *schistacea*.—(1) Change of pace: *schistacea* accelerates throughout; *leucostigma* accelerates and decelerates as measured by pace ratio of sections 2/3. (2) Note shape: *schistacea* notes are flat or slightly rounded; *leucostigma* notes are either partially or entirely chevron shaped. (3) Change in note shape: *schistacea* notes become more rounded and downslurred; *leucostigma* notes maintain shape although initial notes sometimes lack upslur side of chevron. (4) Note duration: *schistacea* notes 1, 2, 3, 4, 5 are longer. (5) Interval duration: *schistacea* intervals 1, 2 are longer. (6) Change in peak frequency: *schistacea* notes increase gradually or are flat in second half of loudsong; corresponding *leucostigma* notes decrease as measured by ratio of peak frequencies 3/5. (7) Chevron-shaped call: found only in *schistacea*.

leucostigma versus *caurensis*.—(1) Number of notes: fewer notes in *caurensis* loudsong. (2) Change of pace: *caurensis* accelerates throughout; *leucostigma* accelerates at a slower rate at beginning and decelerates at end as measured in pace ratio of sections 1/2, 1/3. (3) Note shape: *caurensis* notes are heavily fre-

quency modulated and poorly defined; *leuco-stigma* notes are either partially or entirely chevron shaped. (4) Change in note shape: *caurensis* notes are slightly downslurred initially, but then slightly rounded or shapeless; *leucostigma* notes maintain shape although initial notes sometimes lack upslur side of chevron. (5) Interval duration: *caurensis* intervals are longer throughout as measured in length of intervals 1, 2, 3, 4. (6) Change in interval duration: *caurensis* shortens; *leucostigma* near even spacing as measured in ratio of intervals 1/4, 2/4. (7) Change in peak frequency: *caurensis* first half is flat or decreases gradually and then decreases sharply; *leucostigma* increases and decreases gradually as measured in ratio of peak frequencies 1/3, 1/4, 1/5, 2/4, 2/5, 3/4, 3/5. (8) Long Call: note shape differs.

subplumbea versus *humaythae*.—(1) Peak frequency: *subplumbea* higher through first half of loudsong as measured in peak frequency of notes 1, 2, and 3. (2) Change in peak frequency: *subplumbea* increases and decreases gradually; *humaythae* increases sharply in first quarter of song, then is flat although final 1–3 notes may decrease slightly as measured in ratio of peak frequencies 1/4, 1/5, 2/4, 2/5, 3/5.

subplumbea versus *brunneiceps*.—(1) Pace: Pace of *subplumbea* faster at beginning as measured in pace of section 1. (2) Change of pace: *subplumbea* accelerates at beginning and decelerates at end; *brunneiceps* accelerates throughout as measured in pace ratio of sections 1/3, 2/3. (3) Peak frequency: *subplumbea* lower through much of loudsong as measured in peak frequency of notes 1, 2. (4) Change in peak frequency: *subplumbea* increases and decreases gradually; *brunneiceps* first half to two-thirds flat or nearly so, remaining notes decrease sharply as measured in ratio of peak frequencies 1/3, 2/3.

subplumbea versus *rufifacies*.—(1) Pace: Overall pace: *subplumbea* is faster. (2) Change of pace: *subplumbea* accelerates at beginning and decelerates at end; *rufifacies* accelerates throughout as measured in pace ratio of sections 1/2, 1/3, 2/3. (3) Note shape: Although notes of both are more or less chevron-shaped, notes of *rufifacies* are clearly downslurred throughout first half of songs whereas those of *subplumbea* only occasion-

ally lack upslur in first few notes. (4) Change in note shape: *subplumbea* notes maintain clear shape; *rufifacies* become frequency modulated. (5) Note duration: *subplumbea* notes are shorter initially as measured in length of note 2. (6) Change in note duration: *subplumbea* lengthen or are close to even; *rufifacies* notes shorten as measured in ratio of notes 2/4. (7) Change in peak frequency: *subplumbea* increases and decreases gradually; *rufifacies* increases gradually in first half to two-thirds, remaining notes decrease abruptly and sharply.

subplumbea versus *schistacea*.—(1) Number of notes: fewer notes in *schistacea* loudsong. (2) Note shape: *schistacea* notes are flat or slightly rounded; *subplumbea* notes are chevron shaped. (3) Change in note shape: *schistacea* notes become more rounded and downslurred; *subplumbea* notes maintain shape although initial notes sometimes lack upslur side of chevron. (4) Change in note length: *schistacea* notes shorten; *subplumbea* lengthen or are nearer to even as measured in ratios of notes 1/4, 1/5. (5) Interval length: *schistacea* intervals are longer throughout as measured in length of intervals 1, 2, 3, 4. (6) Change in peak frequency: *schistacea* notes increase gradually or are flat in second half of loudsong; second half notes of *subplumbea* notes decrease to a level lower than initial notes as measured in ratios of peak frequencies 1/4, 1/5, 2/4, 2/5, 3/4, 3/5, 4/5. (7) Chevron-shaped call: found only in *schistacea*.

subplumbea versus *caurensis*.—(1) Number of notes: fewer notes in *caurensis* loudsong. (2) Change of pace: *caurensis* accelerates throughout; *subplumbea* accelerates at a slower rate at beginning and decelerates at end as measured in pace ratio of sections 1/2, 1/3. (3) Note shape: *caurensis* notes are heavily frequency modulated and poorly defined; *subplumbea* notes are chevron shaped. (4) Change in note shape: *caurensis* notes are slightly downslurred initially, but then slightly rounded or shapeless; *subplumbea* notes maintain shape although initial notes sometimes lack upslur side of chevron. (5) Interval duration: *caurensis* intervals are longer throughout as measured in length of intervals 1, 2, 3, 4. (6) Change in peak frequency: *caurensis* first half is flat or decreases gradually and then decreases sharply; *subplumbea* in-

creases and decreases gradually as measured in ratio of peak frequencies 1/3, 2/3, 3/5. (7) Long Call: note shape differs.

humaythae versus *brunneiceps*.—(1) Pace: pace of *humaythae* faster at beginning as measured in pace of section 1. (2) Change of pace: *humaythae* accelerates at beginning and decelerates at end; *brunneiceps* accelerates throughout as measured in pace ratio of sections 1/2, 1/3, 2/3. (3) Note frequency: *humaythae* lower through much of loudsong as measured in peak frequency of notes 1, 2, 3. (4) Change in peak frequency: *humaythae* increases sharply in first quarter of song, then is flat although terminal notes decrease; *brunneiceps* first half to two-thirds flat or nearly so, remaining notes decrease sharply as measured in ratio of peak frequencies 1/3, 1/4, 1/5, 2/3, 2/4, 2/5, 3/4, 3/5.

humaythae versus *rufifacies*.—(1) Change of pace: *humaythae* accelerates at beginning and decelerates at end; *rufifacies* accelerates throughout as measured in pace ratio of sections 1/2, 1/3, 2/3. (2) Note shape: Although notes of both are more or less chevron-shaped, notes of *rufifacies* are clearly downslurred throughout first half of songs whereas those of *humaythae* only occasionally lack upslur in first few notes. (3) Change in note shape: *humaythae* notes maintain clear shape; *rufifacies* become frequency modulated. (4) Note duration: *humaythae* notes are shorter as measured in length of notes 2, 4, 5. (5) Change in note duration: *humaythae* notes lengthen; *rufifacies* notes shorten as measured in ratio of notes 2/3. (6) Interval duration: *humaythae* intervals are shorter throughout most of loudsong as measured in length intervals 1, 2, 3. (7) Peak frequency: *humaythae* lower through much of loudsong as measured in peak frequency of notes 1, 2. (8) Change in peak frequency: *humaythae* increases sharply in first quarter of song, then is flat although terminal notes decrease; *rufifacies* increases gradually in first half to two-thirds, remaining notes decrease abruptly and sharply as measured in ratio of peak frequencies 1/3, 1/4, 1/5, 2/3, 2/4, 2/5, 3/4.

humaythae versus *schistacea*.—(1) Number of notes: fewer notes in *schistacea* loudsong. (2) Change of pace: *schistacea* accelerates throughout; *humaythae* accelerates and decelerates, but pace at end slower than beginning

as measured in pace ratio of sections 1/3. (3) Note shape: *schistacea* notes are flat or slightly rounded; *humaythae* notes are chevron shaped. (4) Change in note shape: *schistacea* notes become more rounded and downslurred; *humaythae* notes maintain shape although initial notes sometimes lack upslur side of chevron. (5) Change in note duration: *schistacea* notes shorten or are close to even; *humaythae* notes lengthen in first half of loudsong as measured in ratio of notes 2/3. (6) Interval duration: *schistacea* intervals are longer throughout as measured in length of intervals 1, 2, 3, 4. (7) Change in peak frequency: *schistacea* increases very gradually throughout or initially increases and becomes flat; *humaythae* increases sharply in first quarter of song, then is flat although terminal notes decrease as measured in ratios of peak frequencies 2/3, 4/5. (8) Chevron-shaped Call: found only in *schistacea*.

humaythae versus *caurensis*.—(1) Number of notes: fewer notes in *caurensis* loudsong. (2) Change of pace: *caurensis* accelerates throughout; *humaythae* accelerates at a slower rate at beginning and decelerates at end as measured in pace ratio of sections 1/2, 1/3. (3) Note shape: *caurensis* notes are heavily frequency modulated and poorly defined; *humaythae* notes are chevron shaped. (4) Change in note shape: *caurensis* notes are slightly downslurred initially, but then slightly rounded or shapeless; *humaythae* notes maintain shape although initial notes sometimes lack upslur side of chevron. (5) Interval duration: *caurensis* intervals are longer throughout as measured in length of intervals 1, 2, 3, 4. (6) Change in interval duration: *caurensis* shortens; *humaythae* near even spacing as measured in ratio of intervals 1/4, 2/4. (7) Peak frequency: *caurensis* initially higher as measured in peak frequency of note 2. (8) Change in peak frequency: *caurensis* first half is flat or decreases gradually and then decreases sharply; *humaythae* increases sharply in first quarter of song, then is flat although terminal notes decrease as measured in ratio of peak frequencies 1/3, 1/4, 1/5, 2/3, 2/4, 2/5, 3/4, 3/5. (9) Long Call: note shape differs.

brunneiceps versus *rufifacies*.—(1) Change of pace: both accelerate throughout, but *rufifacies* accelerates at a faster rate towards end as measured in pace ratio of sections 2/3. (2)

Change in note shape: *brunneiceps* notes maintain clear shape; *rufifacies* become frequency modulated. (3) Peak frequency: *brunneiceps* higher through much of loudsong as measured in peak frequency of notes 1, 2, 3. (4) Change in peak frequency: *brunneiceps* first half to two-thirds flat or nearly so, remaining notes decrease sharply; *rufifacies* increases gradually in first half to two-thirds, remaining notes decrease abruptly and sharply as measured in ratio of peak frequencies of 2/3.

brunneiceps versus *schistacea.*—(1) Number of notes: fewer notes in *schistacea* loudsong. (2) Note shape: *schistacea* notes are flat or slightly rounded; *brunneiceps* notes are more or less chevron shaped. (3) Change in note shape: *schistacea* notes become more rounded and downslurred; *brunneiceps* notes are mostly downslurred in initial half, but then shaped like chevrons. (4) Change in note duration: *schistacea* notes shorten throughout; *rufifacies* notes shorten initially, but are of even length toward end as measured in ratios of notes 4/5. (5) Interval duration: *schistacea* intervals are longer throughout as measured in length of intervals 1, 2, 3, 4. (6) Change in interval duration: *schistacea* intervals are near even in length; *brunneiceps* intervals shorten as measured in ratio of intervals 1/3, 1/4, 2/3, 2/4. (7) Note frequency: *schistacea* lower throughout most of loudsong as measured in peak frequency of notes 1, 2, 3. (8) Change in peak frequency: *schistacea* increases gradually throughout or initially increases and becomes flat; *brunneiceps* first half to two-thirds flat or nearly so, remaining notes decrease sharply as measured in ratio of peak frequencies 1/4, 1/5, 2/4, 2/5, 3/4, 3/5, 4/5. (9) Chevron-shaped Call: found only in *schistacea.*

brunneiceps versus *caurensis.*—(1) Number of notes: fewer notes in *caurensis* loudsong. (2) Note shape: *caurensis* notes are heavily frequency modulated and poorly defined; *brunneiceps* notes are more or less chevron shaped. (3) Change in note shape: *caurensis* notes are slightly downslurred initially, but then slightly rounded or shapeless; *brunneiceps* notes are mostly downslurred in initial half, but then shaped like chevrons. (4) Interval duration: *caurensis* intervals are longer throughout as measured in length of intervals 1, 2, 3, 4. (5) Peak frequency: *caurensis* lower throughout most of loudsong as measured in peak frequency of notes 2, 3, 4. (6) Long Call: note shape differs.

rufifacies versus *schistacea.*—(1) Number of notes: fewer notes in *schistacea* loudsong. (2) Change of pace: *schistacea* accelerates throughout; *rufifacies* also accelerates throughout but pace at end much faster than beginning as measured in pace ratio of sections 1/3. (3) Note shape: *schistacea* notes are flat or slightly rounded; *rufifacies* notes are more or less chevron shaped. (4) Change in note shape: *schistacea* notes become more rounded and downslurred; *rufifacies* notes are mostly downslurred in initial half, but then shaped like chevrons and becoming frequency modulated. (5) Interval duration: *schistacea* intervals are longer in second half; as measured in length of intervals 3, 4. (6) Change in interval duration: *schistacea* intervals near even in length; *brunneiceps* intervals shorten more as measured in ratio of interval 2/3. (7) Change in peak frequency: *schistacea* increases gradually throughout or initially increases and becomes flat; *rufifacies* increases gradually in first half to two-thirds, remaining notes decrease abruptly and sharply as measured in ratio of peak frequencies 1/4, 1/5, 2/4, 2/5, 3/4, 3/5. (8) Chevron-shaped Call: found only in *schistacea.*

rufifacies versus *caurensis.*—(1) Note shape: *caurensis* notes are heavily frequency modulated and poorly defined; *rufifacies* notes are more or less chevron shaped. (2) Change in note shape: *caurensis* notes are slightly downslurred initially, but then slightly rounded or shapeless; *rufifacies* notes are mostly downslurred in initial half, but then shaped like chevrons and becoming frequency modulated. (3) Note duration: *caurensis* notes are longer throughout as measured in length of notes 1, 2, 3, 4, 5. (4) Interval duration: *caurensis* intervals are longer throughout as measured in length of intervals 1, 2. (5) Change in peak frequency: *caurensis* first half is flat or decreases gradually and then decreases sharply; *rufifacies* increases gradually in first half to two-thirds, remaining notes decrease abruptly and sharply as measured in ratio of peak frequencies 1/3, 1/5, 2/3, 2/5. (6) Long Call: note shape differs.

schistacea versus *caurensis.*—(1) Note shape: *schistacea* notes are flat or slightly

rounded; *caurensis* notes are heavily frequency modulated and poorly defined. (2) Change in note shape: *schistacea* notes become more rounded and downslurred but maintain a clear shape; *caurensis* notes are slightly downslurred initially, but then slightly rounded or shapeless. (3) Note duration: *schistacea* notes 1, 2, 3 are longer. (4) Interval duration: *schistacea* intervals 1, 2 are shorter. (5) Change in interval duration: *schistacea* intervals remain near even in length; *caurensis* intervals shorten more as measured by ratios of intervals 1/3, 1/4, 2/3, 2/4. (6) Change in peak frequency: *schistacea* increases gradually throughout or initially increases and becomes flat; *caurensis* first half is flat or decreases gradually and then decreases sharply as measured by ratios of maximum frequencies 1/4, 1/5, 2/4, 2/5, 3/4, 3/5. (7) Long Call: note shape differs. (8) Chevron-shaped Call: found only in *schistacea*.

APPENDIX 2

Recordings Examined.—The following list identifies recordings used in the study by taxon, country, state or department, recording location, and recordist. Numbers following the recordist name identify the number of cuts per recordist per location. Acronyms for recording archives: ML = Macaulay Library, Cornell Laboratory of Ornithology, Ithaca; NSA = National Sound Archive, The British Library, London. ISL = recordings not yet archived in an institutional collection but that have been copied into the inventory maintained by Morton and Phyllis Isler. Many of these unarchived recordings either are in the process of being archived or will eventually be archived by the recordists. Nomenclature reflects recommended taxonomic position.

Percnostola s. saturata: (8 recordings; 2 localities). Guyana: Kaieteur Fall (Braun 2 ISL), Mount Roraima (Braun 2 ISL, Milensky 2 ISL, Robbins 2 ISL).

P. s. obscura: (16 recordings; 1 locality). Venezuela: Bolívar; La Escalera (Ascanio 1 ISL, Behrstock 1 ISL, Gullick 2 NSA, Whittaker 3 ISL, Zimmer 9 ISL).

Percnostola l. leucostigma: (57 recordings; 17 localities). Brazil: Amazonas; Manaus, 40–90 km N of (Bierregaard 2 ML, Cohn-Haft 3 ML, Stouffer 1 ML, Whittaker 4 ISL). Guyana: Acarai Mountains (Robbins 2 ISL), Bar-

amita (Robbins 3 ISL), Bartica (Finch 2 ISL), Corona Falls (Finch 1 ML), Dubulay Ranch (Robbins 2 ISL), Iwokrama Forest Reserve (Robbins 3 ISL, Whitney 2 ISL), Kaieteur Fall (Finch 1 ML, Milensky 2 ISL), Onoro River (Braun 2 ISL), Sipu River (Braun 4 ISL), Waruma River (Robbins 5 ISL). Suriname: Brownsberg Nature Reserve (Whitney 1 ISL), Kabalebo Nature Reserve (Whitney 1 ISL), Location unknown (Donahue 1 NSA), Raleigh Vallen (Whitney 1 ISL). Venezuela: Bolívar; El Dorado-La Escalera Road (Ascanio 1 ISL, Macaulay 1 ML, Whitney 1 ISL), La Escalera (Ascanio 1 ISL, Behrstock 1 ISL, Gadd 1 NSA, Gibbs 1 NSA, Innis 1 NSA, D. Willis 3 NSA, Zimmer 3 ISL).

P. l. infuscata: (18 recordings; 4 localities). Brazil: Amazonas; Jaú, P. N. de (Cohn-Haft 2 ISL, K. Rosenberg 1 ISL, Pacheco 1 ISL, Whittaker 1 ISL), São Gabriel da Cachoeira (Whittaker 5 ISL, Zimmer 3 ISL), São Gabriel da Cachoeira, across river from (Whitney 2 ISL, Whittaker 1 ISL, Zimmer 1 ISL). Colombia: Vaupés; Mitú (Hilty 1 ISL).

P. l. subplumbea: (110 recordings; 37 localities). Brazil: Acre; Amônea, Rio (Whitney 1 ISL, presumably this taxon), Boca de Tejo (Whittaker 1 ISL, presumably this taxon), Branco, Rio (Whitney 1 ISL), Minas Gerais 2 (Whitney 1 ISL, presumably this taxon), Serra do Divisor, P. N. (Whitney 4 ISL); Amazonas; Cruzeiro do Sul/Santa Barbara Road (Whitney 1 ISL), Palmarí, R. N. (Whitney 9 ISL, Zimmer 8 ISL). Colombia: Amazonas; Amacayacú, P. N. (Whitney 3 ISL, Willis 1 NSA, tentatively assigned to this taxon). Ecuador: No location (Wall 1 ML); Morona-Santiago; Miazal (Whitney 2 ISL), Santiago, Río (Robbins 1 ML), Taisha (Robbins 1 ML); Napo; Coca (Macaulay 1 ML, Robbins 1 ML), Jatun Sacha (Lewis 2 NSA), La Selva Lodge (Behrstock 2 ISL, G Rosenberg 4 ISL), Limoncocha (Coffey 1 ISL), Loreto, 15–60 km west (Whitney 5 ISL), Maxus Road (Krabbe 5 ISL), Sacha Lodge (Behrstock 1 ISL, Fisher 1 MSA), Suno, Río (Whitney 1 ISL), Tiputini Station (Arvin 4 ISL, Zimmer 3 ISL); Pastaza; Kapawi Lodge (Krabbe 1 ISL). Peru: Amazonas; Huampami (Parker 1 ML); Loreto; Buenavista, Quebrada (Lane 1 ISL), Corrientes, Río (Alvarez 2 ISL), Explorama Lodge (Whitney 2 ISL), Iquitos (Donahue 1 ML), Jeberos (Lane 1 ISL), Libertad (G. Rosenberg 1

ISL), Morona, Río (Lane 1 ISL), Pichana (Whittaker 1 ISL), Sucusari, Quebrada (M. Isler 2 ML, P. Isler 7 ML, Michael 1 ISL, Parker 5 ML, G. Rosenberg 2 ISL, Whitney 2 ISL), Tahuayo Lodge (Hornbuckle 2 ISL), Varillal (Whitney 1 ISL, Whittaker 1 ISL), Yanamono (Donahue 1 ML, Whitney 3 ISL), Yarapa Reserve (Michael 1 ISL); San Martín; Shapaja Road (Lane 2 ISL); Ucayali; Abujao (Meyer 2 ISL).

P. l. intensa: (0 recordings).

Percnostola humaythae: (20 recordings; 10 localities). Bolivia: Pando; Camino Mucden (Parker 2 ML), Chive (Rocha 1 ISL). Brazil: Acre; Humaitá Reserve (Whitney 1 ISL); Amazonas; Amazon Lodge (Zimmer 1 ISL), Benjamin Constant (Whitney 4 ISL), Humaitá (Whitney 2 ISL), Ipixuna, Rio (Whitney 1 ISL), Lábrea (Whitney 1 ISL), Tefé (Coopmans 1 ML), Vila Democracia (Whitney 4 ISL).

Percnostola brunneiceps: (16 recordings; 6 localities). Peru: Cuzco; Consuelo (O'Shea 1 ISL), Quimbiri (Widdowson 1 ISL), Pilcopata (Whitney 1 ISL); Madre de Dios; Amazonia Lodge (Arvin 1 ISL, Innes 1 ISL, Lloyd 1 ISL, R. & V. Yavar 1 ISL, Walker 1 ISL, Whitney 2 ISL). Bolivia: La Paz; Alto Madidi (Hennessey, 3 ISL), Tuichi, Río (Whitney 3 ISL).

Percnostola rufifacies: (58 recordings; 20 localities). Brazil: Amazonas; Atininga, Rio (Whitney 1 ISL), Ipixuna, Rio (Whitney 1 ISL), Mapía, Rio (Zimmer 2 ISL), Paxurizal (Whitney 1 ISL), Pousada Rio Roosevelt, left bank (Whittaker 3 ISL), Sucunduri (Whitney

1 ISL); Mato Grosso; Cristalino, Rio (Whitney 4 ISL; Zimmer 2 ISL); Pará; Altamira, right bank 15 km S (Whitney 1 ISL), Apaçy (Whitney 2 ISL), Aveiro (Whitney 3 ISL), Aveiro, islands between Apaçy and Aviero (Whitney 4 ISL), Carajas, Serra dos (Zimmer 1 ISL), Caxiuanã (Whitney 8 ISL; Whittaker 5 ISL; Zimmer 2 ISL), Itapoama (Whitney 3 ISL), Santarém (Whittaker 3 ISL), Vila Braga (Whitney 1 ISL); Rondônia; Caracol, Rio (Whitney 2 ISL), Pardo, Rio (Zimmer 1 ISL), Porto Velho (Whitney 2 ISL), Rancho Grande, Fazenda (Whittaker 2 ISL; Zimmer 3 ISL).

Percnostola schistacea: (65 recordings, 17 localities). Brazil: Acre; Boca de Tejo (Whittaker 3 ISL), Igarapé Ouro Preto (Whitney 5 ISL), P. N. da Serra do Divisor (Whitney 5 ISL), Riozinho das Minas (Whitney 3 ISL); Amazonas; Barro Vermelha (Whittaker 1 ISL), Benjamin Constant (Whitney 5 ISL), R. N. Palmarí (Whitney 2 ISL, Zimmer 1 ISL). Colombia: Amazonas; P. N. Amaca-yacú (Whitney 4 ISL). Ecuador: Sucumbios; Cuyubeno (J. Rowlett 1 ISL, Whitney 1 ISL). Peru: Loreto; Colonia Angamos (Lane 1 ISL), Pichana (Zimmer 1 ISL), Quebrada Orán (Whitney 4 ISL), Quebrada Sucusari (Budney/Parker 2 ML, Parker 3 ML, P. Isler 1 ML, Whitney 12 ISL), Santa Cecilia (Robbins 1 ML), Yanamono (Whitney 2 ISL); Ucayali; Abujao (Meyer 1 ISL, O'Neill 1 ISL), Cerro Tahuayo (Meyer 5 ISL).

Percnostola caurensis caurensis: (0 recordings).

Percnostola c. australis: (23 recordings; 1 locality). Venezuela: Bolívar; Cerbatana, Serranía de (Zimmer 23 ISL).